PROC. R. SOC. VICT. vol. 97, no. 4, 175-178, December 1985

FIRST RECORD OF WELL-PRESERVED MEGAFOSSILS OF *NOTHOFAGUS* FROM MAINLAND AUSTRALIA

By D.C. CHRISTOPHEL

Botany Department, University of Adelaide, G.P.O. Box 498, Adelaide, South Australia, 5001

ABSTRACT: Mummified leaves, cupules and seeds of *Nothofagus* (Fagaceae) have been recovered from the Miocene Bacchus Marsh Locality in Victoria, Australia. Preliminary numerical analysis of the leaves suggests one diverse species present with no close similarities to any extant Australian species of *Nothofagus*. Also no strong similarities are initially apparent to any of the fossil species recently described from Tasmania. Both leaves and cupules support assignment of the fossils to either section *Calusparassus* or section *Nothofagus* subsection *Quadripartite* of *Nothofagus*.

Biogeographic considerations of Gondwanaland frequently include discussions of *Nothofagus* (Raven & Alexfod 1972, van Steenis 1972, Cracraft 1975, Schuster 1976, Humphries 1981). These discussions are usually based on distribution of extant species, as the fossil record of the genus — particularly the megafossil record — has been far from adequate. These discussions have therefore rarely brought forward definitive solutions to the problems of evolution and radiation of species within the genus. Australia has been particularly perplexing in this regard in that while a diverse, and indeed frequently dominant, fossil pollen record for *Nothofagus* in the Tertiary is known (Kemp 1978, Martin 1982), no confirming megafossil evidence had been forthcoming (Christophel & Blackburn 1978). Megafossil remains of *Nothofagus* have been recently described from Tasmania (Hill 1983 a, b, 1984), but prior to this report, no organically-preserved megafossil remains were known from continental Australia. Some fossils of *Nothofagus* have been reported from continental Australia in the past (e.g. Paterson 1935) but in all cases cuticular remains were either not present or not reported. Coupled with the fact that the fossils in many of these reports were found in course sediments where venation detail is not preserved well, the identification of those fossils must remain questionable.

LOCALITY

The fossils described in this report were collected in early 1984 from the overburden at the Maddingley Coal Mine in Bacchus Marsh, Victoria, Australia (37°41′S, 144°36′E). The leaves and fruits occur as part of a grey-brown carbonaceous clay lens occurring 2 m above the surface of the coal seam. This coal seam is considered to be a part of the Tertiary Werribee Formation (Abele 1976, Roberts 1984).

The palynoflora of the clay lens has been identified as belonging to the *Triporopollenties bellus* zone of Stover and Partridge (1973) by A. Partridge, Esso of Australia (pers. comm.), based on the frequency of *T. bellus*. While this zone was originally considered to be Middle to Late Miocene, foraminiferal evidence from the Murray Basin indicates an Early Miocene age for it (W.K. Harris, Western Mining Corp., pers. comm.). This dating places the Bacchus Marsh clay in the same zone as the Yallourn Clay of the Latrobe Valley coal system (Luly, Sluiter & Kershaw 1980).

MATERIALS AND METHODS

The mummified leaves and fruits were recovered by macerating blocks of the clay in hot 20% W/V H_2O_2 and sieving the resultant slurry. In this manner over 150 mummified leaves and fruits were recovered. The commonest leaf type is a simple, serrate, craspedodromous angiosperm which, based on venation, stomatal arrangement and trichome types was readily assignable to *Nothofagus* (Fig. 1a). The dominant fruit type recovered was a four parted cupule, occasionally complete with three seeds, which was also readily assignable to *Nothofagus* (Fig. 1b). The 24 most complete fossil leaves were selected for morphological examination. These leaves have a large range of lengths (1.2-5.1 cm) with several fragmentary specimens having a projected length of greater than 7 cm. Seven leaves had lengths very near the minimum, giving a significant difference between the mean and median length values. This size distribution might be interpreted as more than one species present, or a number of juvenile leaves in the sample, or reproductive leaf dimorphism such as that demonstrated by Hill for *Nothofagus moorei* (Hill 1983b).

A preliminary numerical analysis of the leaves, and leaves from 11 extant species of *Nothofagus* from section *Nothofagus* and section *Calusparassus* subsection *Quadripartite* was carried out using many of the characters proposed by Hill (1983a) and the distance metric of Blackburn (1980). A list of the characters used is presented in Table 1. Most were taken directly from Hill's analysis of *Nothofagus* (1983a) but several were slightly modified to provide cut-off points for character states more consistent with the current data set. Several of Hill's characters were omitted because the OTUs for this analysis did not display features used in his analysis. Specifically the Type Three trichome of Hill was not

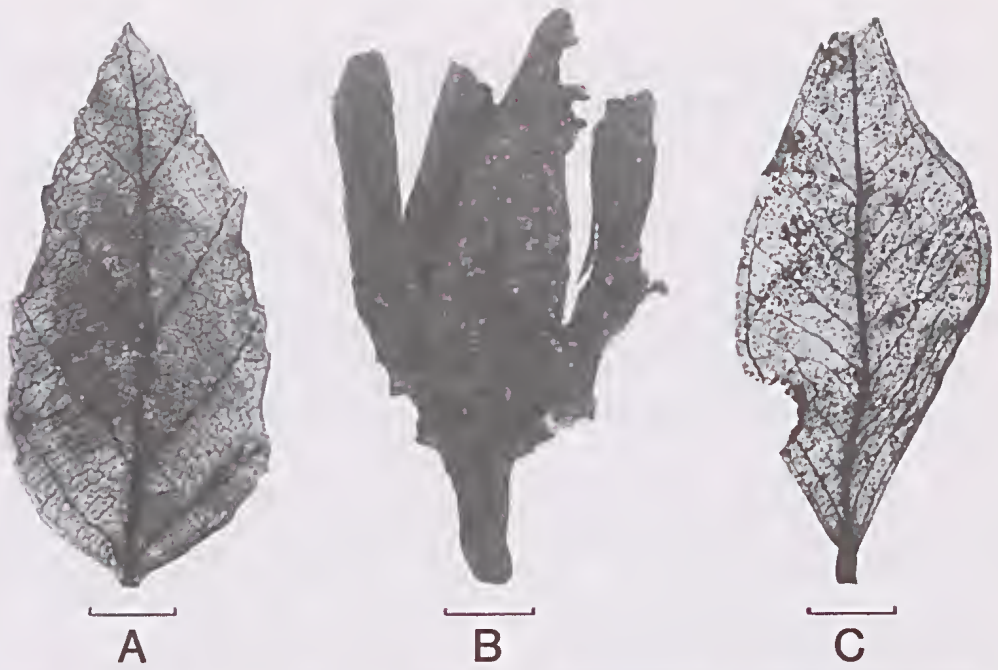

Fig. 1—Megafossils from Baeehus Marsh, Australia. A, Fossil leaf of *Nothofagus* showing eraspedodromous secondary venation and pereurrent tertiary venation. Scale bar equals 4 mm. B, Fossil fruit eupule of *Nothofagus* showing four parts. Scale bar equals 1.7 mm. C, Fossil Myrtaeeous leaf. Seale bar equals 3.5 mm.

present in the Baeehus Marsh fossils or in the extant species included, and henee eharaeters relating to them were dropped. A dendrogram was then constructed using the UPGMA clustering algorithm (Fig. 2). Leaves of extant speeies from seetion *Calusparassus* subseetions *Bipartite* and *Tripartite* were omitted from the analysis as all leaves were obviously toothed, all the cupules were four parted and they contained three seeds.

RESULTS AND DISCUSSION

While the preliminary nature of this analysis must be emphasised, several observations may be made from the results (Fig. 2). Firstly it may be seen that 22 of the 24 fossils eluster together (or at least are more similar to each other than to leaves of any extant speeies ineluded). By observing the relative level at which the dimorphic leaves of *Nothofagus moorei* elustered, it becomes

TABLE 1

CHARACTERS SCORED FOR EXTANT AND FOSSIL OF LEAVES *Nothofagus*. STATE 1 OF EACH CHARACTER IS EXPRESSED IN THE TABLE. CHARACTERS WITH AN ASTERISK ARE FROM HILL (1983a).

*	1.	Adaxial glandular triehome bases present
*	2.	Adaxial non glandular trichome base present
*	3.	Abaxial glandular triehome bases present
*	4.	Abaxial non glandular triehome bases present
*	5.	Giant stomates present
*	6.	Subsidiary cells irregularly thickened
	7.	Abaxial epidermal cells convoluted walls
*	8.	Less than 12 secondary veins (pairs)
*	9.	Secondary veins straight for greater than or equal to ⅔ of length
	10.	Secondary vein angle of divergence from primary vein 45°
*	11.	Intersecondary veins present
*	12.	Tertiary veins percurrent, obliquc, convex
*	13.	Serrations glandular or spinose
*	14.	Serrations only in upper ½-⅓
*	15.	Tooth sinus angular
	16.	Principal tooth vein ramified
*	17.	Serrations 2 per secondary vein interval
*	18.	Leaf length less than 4 cm.

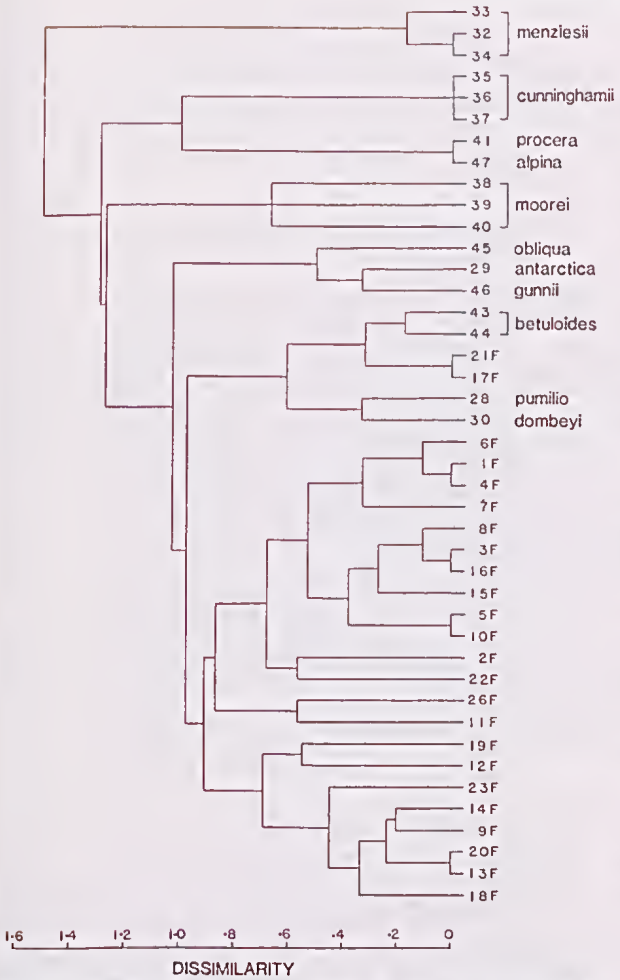

Fig. 2—UPGMA dendrogram of the 11 extant species and 24 fossil specimens of *Nothofagus*. Each number on the vertical axis (OTU's) represents one leaf. A number followed by an "F" represents fossil leaves from Bacchus Marsh, Victoria.

reasonable to interpret the 22 as a single variable taxon. The two remaining fossil leaves (Fig. 2 — 17F and 21F) cluster most closely with the South American *Nothofagus betuloides*. The significance of this may be diluted by the fact that these two fossil specimens are missing their lamina bases, and hence several characters were unscored for them. A final observation from Fig. 2 is that the three Australian species, *N. moorei, N. cunninghamii* and *N. gunnii*, show no great similarity to the Bacchus Marsh fossils. Clearly an additional analysis incorporating more specimens of some extant species and also including several extant species which had not been available for this analysis is indicated before definite conclusions on the relationships of the Bacchus Marsh fossils can be made.

A non-numerical comparison with the fossil species described by Hill from Tasmania deposits (1983a, b, 1984) based on their published descriptions was also undertaken. These fossils were not included in the numerical analysis because data on individual leaves from those taxa were not available and it was considered undesirable to include an aggregate OTU with a set in which all others were individual leaves. Using architectural features, the lack of a fimbrial vein and the size variability displayed by the Bacchus Marsh fossils make them most similar to *Nothofagus johnstonii* Hill. However, the tooth/secondary vein ratio of 2.0 for the Bacchus Marsh fossils, as well as several other architectural features differ from the descriptions of *N. johnstonii*.

The cuticular features of the Bacchus Marsh fossils are also different from those described for the Tasmanian fossil *Nothofagus*. The Bacchus Marsh fossils have the typical cyclocytic arrangement of subsidiary cells, but unlike *Nothofagus johnstonii* Hill and *N. tasmanica* Hill, they do not exhibit pronounced cuticular thickenings on the subsidiary cells. Of the trichome types described by Hill (1983a), the complex glandular trichome and the non-glandular type with a heavily-cutinized circular foot cell and a simple hair are both commonly found on abaxial and adaxial surfaces of the Bacchus Marsh fossils. The non-glandular type is particularly dense on the adaxial (non-stomatal) surface over veins and the margin. The other trichome types described by Hill have not been observed on the Bacchus Marsh fossils on either leaf surface. This combination of epidermal features does not match particularly well with any of the fossil Tasmanian species.

As only a solitary cupule from one Tasmanian fossil species has been described to date, and as cupules of several of the relevant extant species have yet to be obtained, no comparisons for the fruits are made. Seeds recovered from the Bacchus Marsh deposit are not preserved sufficiently well for comparisons to be made with extant material.

The overall diversity of the megafossil flora at Bacchus Marsh is relatively low. The second commonest leaf type has affinities with the Myrtaceae (Fig. 1c). Two angiosperm leaf types of unknown affinities have also been recovered, as well as one Araucariaceae twig and several leaves presumed to belong to the Podocarpaceae. Two other fruit types also commonly occur in the deposit, but they have not yet been identified.

Despite the apparent dissimilarity of the *Nothofagus* leaves, the remainder of the Bacchus Marsh flora has elements in common with the Tasmanian Pioneer flora of a similar age. The Pioneer flora is also of a reasonable low diversity, has several coniferous taxa and Myrtaceae leaves are also represented (Hill & Macphail 1983). These same elements are also present in the Miocene Yallourn deposit of Victoria, although *Nothofagus* megafossils have not been reported from that locality.

The discovery of abundant organically-preserved *Nothofagus* megafossils at the Bacchus Marsh locality provides the first supportive evidence from mainland Australia for the "*Nothofagus* flora" which the palynological record has suggested was dominant in the Tertiary. The predominance of microphyllous leaves and the low diversity of the flora are consistent with a cool-temperate forest vegetation. Such a vegetation type

could alternatively be found, however, at a higher altitude in a slightly warmer temperate region. Hill (1983) suggested that information about fossil *Nothofagus* on mainland Australia was crucial to the study of evolution within the genus. The discovery of the Bacchus Marsh flora with its abundant *Nothofagus* remains should therefore aid in the continuance of evolutionary studies within the genus and provide additional data with which to test some of the relationships between taxa hypothesized by Hill (1983, 1984).

As more and more records of *Nothofagus* megafossils become documented, perhaps the statement of Patterson (1980) that "*Nothofagus* is uninformative on the interrelationships of the southern hemisphere areas" can ultimately be challenged.

ACKNOWLEDGEMENTS

I acknowledge the support of Alcoa of Australia and the Australian Research Grants Scheme for grant E83/15626. I also acknowledge I. McCloud, Maddingley Coal Co., for permission to collect material, A. Bennett, A. Fuller and A. Renfrey for assistance in data collection, A. Moore for adapting the UPGMA algorithm to my research computer and Jane Purcell for preparation of the plates. I also wish to thank R.S. Hill for useful comments on the original manuscript.

REFERENCES

Abele, C., Gloe, C.S., Hocking, J.B., Holdgate, G., Kenley, P.R., Lawrence, C.R., Ripper, D. & Threlfall, W.F., 1976. Tertiary. In *Geology of Victoria*, J.G. Douglas & J.A. Ferguson, eds, Geological Society of Australia, Special Publ. 5:177-274.

Blackburn, D.T., 1981. A generalized distance metric for the analysis of variable taxa. *Bot. Gaz.* 141 (3): 325-335.

Christophel, D.C. & Blackburn, D.T., 1978. Tertiary megafossil flora of Maslin Bay, South Australia: a preliminary report. *Alcheringa* 2: 311-319.

Cracraft, J., 1975. Historical biogeography and earth history: perspectives for a future synthesis. *Ann. Mo. Bot. Gard.* 62: 227-250.

Hill, R.S., 1983a. *Nothofagus* macrofossils from the Tertiary of Tasmania. *Alcheringa* 7: 169-183.

Hill, R.S., 1983b. *Nothofagus cunninghamii* evolution and its relationship to *N. moorei* as inferred from Tasmanian macrofossils. *Aust. J. Bot.* 31: 453-465.

Hill, R.S., 1984. Tertiary *Nothofagus* macrofossils from Cethana, Tasmania. *Alcheringa* 8: 81-86.

Hill, R.S., & Macphail, M.K., 1983. Reconstruction of the Oligocene vegetation at Pioneer, northeast Tasmania. *Alcheringa* 7: 281-299.

Humphries, C.J., 1981. Biogeographical methods and the southern beeches. In *The Evolving Biosphere*, P.L. Forey, ed., Cambridge Univ. Press, Cambridge, 283-297.

Kemp, E.M., 1978. Tertiary climatic evolution and vegetation history in the south-east Indian Ocean region. *Palaeogeogr. Palaeoclim. Palaeoecol.* 24: 169-208.

Luly, J., Sluiter, I.R. & Kershaw, A.P., 1980. *Pollen Studies of Tertiary Brown Coals: Preliminary Analyses of Lithotypes within the LaTrobe Valley, Victoria.* Monash Publications in Geography 23. Monash University, Melbourne, 1-78.

Martin, H.A., 1982. Changing Cenozoic barriers and the Australian palaeobotanical record. *Ann. Mo. Bot. Gard.* 69: 625-667.

Paterson, H.T., 1935. Notes on plant remains from South Gippsland. *Proc. R. Soc. Vict.* 48: 67-74.

Patterson, C., 1980. Methods of Palaeobiogeography. In *Vicariance Biogeography: A Critique*, G. Nelson & D.E. Rosen, eds, Columbia University Press, New York, 446-550.

Raven, P.H., & Axelrod, D.I., 1972. Plate tectonics and Australian palaeobiogeography. *Science* 176: 1379-1386.

Roberts, P.S., 1984. Explanatory notes on Bacchus Marsh and Ballan 1: 50000 Geological Maps. *Geol. Survey of Victoria Report* 76: 1-102.

Schuster, R.M., 1976. Plate tectonics and its bearing on the geographical origin and dispersal of angiosperms. In *Origin and Early Evolution of Angiosperms*, C.B. Beek, ed., Columbia Univ. Press, New York, 48-138.

Stover, L.E. & Partridge, A.D., 1973. Tertiary and late Cretaceous spores and pollen from the Gippsland Basin, south-eastern Australia. *Proc. R. Soc. Vict.* 85:237-286.

van Steenis, C.G.G.J., 1972. In *Taxonomy, Phytogeography and Evolution*, D.H. Valentine, ed., Academic Press, London, 275-288.